RESEARCH ARTICLE

Low litter cover, high light availability and rock cover favour the establishment of *Ailanthus altissima* in forests in southern Switzerland

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Abstract

Future forest composition is uncertain in many areas due to climate change. The spread of non-native species adds to these uncertainties, particularly in forests recently colonised by novel tree species. To anticipate future forest composition, and thus the provision of ecosystem services, a thorough understanding of the factors influencing the establishment of non-native tree species is essential. We studied the presence and abundance of regeneration of *Ailanthus altissima* (Mill.) Swingle in 89 plots on a regular grid in three sites in southern Switzerland to determine the main drivers of its establishment. All sites are located in abandoned, i.e. currently unmanaged stands of *Castanea sativa* Mill. Propagule pressure is caused by single mature *A. altissima* that colonised the area ca 40 years ago. We found high rock cover, low litter cover and high light availability to be the most important predictors for the presence of *A. altissima* regeneration, whereas its abundance was positively influenced by high light availability, low litter cover and high browsing on regeneration of competing species. However, the presence models performed much better than the abundance models. Interestingly, the most important factors favouring the establishment of *A. altissima* in recently undisturbed sites were found to be similar in a nearby site after a severe forest fire, which suggests a similar establishment strategy after a disturbance as in recently undisturbed forests. Based on our results we expect a further expansion of the species in lowland forests currently dominated by *C. sativa*, likely controlled primarily by light availability.

Keywords

Introduction

Many forest ecosystems are expected to face compositional changes as a consequence of climate change, the introduction and spread of novel tree species, or interactions thereof (Lindner et al. 2010; Hickler et al. 2012). As shifts in tree species composition are first detectable in the regeneration layer (Grund et al. 2005; Moser et al. 2010; Fisichelli et al. 2013; Rigling et al. 2013), a thorough understanding of the factors underlying the successful establishment of novel tree species is crucial to anticipate future community development. Knowledge on the possible future forest composition is a prerequisite for evidence-based, anticipatory management decisions (Lindner et al. 2014), which may enable a continuous provisioning of forest ecosystem services (Gret-Regamey et al. 2013; Seidl et al. 2016). This is particularly important in forests that have only recently started to be colonised by non-native trees, i.e. where the future development is often highly uncertain.

The establishment of non-native tree species has mainly been studied in disturbed forest ecosystems (e.g., Maringer et al. 2012). On the one hand, because colonisation rates are generally slow in closed-canopy forests due to extended periods without gap formation and thus colonisations are difficult to detect and quantify at early stages (Martin et al. 2009; Essl et al. 2011; Wangen and Webster 2006). On the other hand, the majority of non-native tree species that are able to establish and spread outside of their native range are shade intolerant (Martin et al. 2009) and thus depend on large scale disturbances for their establishment. However, also disturbance dependent non-native trees have been able to persist in patches of undisturbed forests. *Prunus serotina* Ehrh., for example, can maintain a short-lived seedling bank, which enables the species to reach the canopy after gap formation (Closset-Kopp et al. 2007; Vanhellemont et al. 2009). Furthermore, *Acacia dealbata* Link, generally considered to be light demanding, was found to be able to grow below the canopy of native trees in south-central Chile (Fuentes-Ramírez et al. 2011).

In this study, we focus on the establishment of the early-successional tree species *Ailanthus altissima* (Mill.) Swingle. Its spread in forest ecosystems has often been associated with disturbances induced by forest management (Call and Nilsen 2003; Radtke et al. 2013; Berg et al. 2017; Rebbeck et al. 2017) or natural processes (Xi 2008; Maringer et al. 2012; Kasson et al. 2013). Despite the positive association of *A. altissima* with disturbance, the species also proved to be capable of establishing in forests lacking a large scale disturbance by virtue of its fast juvenile height growth (Knapp and Canham 2000; Martin et al. 2010; Knüsel et al. 2016). However, the environmental factors underlying the successful establishment of *A. altissima* in recently undisturbed forests remained largely unexplored. To shed light on these factors, we studied its generative regeneration in recently unmanaged lowland forests of southern Switzerland that started to be colonised by *A. altissima* following the general abandonment of the forests dominated by *Castanea sativa* Mill. in the 1950s. Specifically, we focused on the current distribution frontier where only few canopy *A. altissima* are present, which enabled us to study generative regeneration rather than vegetative sprouts that typically grow faster and can persist in shadier conditions (Kowarik 1995; Knüsel et al. 2016). We addressed the following research questions:

i) What are the most important environmental factors that drive the presence and abundance of regeneration of *A. altissima* in recently undisturbed forests?

Once identified, we compared these factors with the environmental drivers of the post-fire establishment of *A. altissima* in the same study region (Maringer et al. 2012), leading to the second research question:

ii) What are the key differences in the environmental drivers of the establishment of *A. altissima* in disturbed versus recently undisturbed forests?

Knowledge on key differences in the establishment requirements of *A. altissima* in forests after a disturbance versus recently undisturbed forests may facilitate predictions on the spread of the species.

Materials and methods

Study species

Ailanthus altissima is a dioecious early successional tree species originating from China that was brought to Europe around the 1740s as an ornamental tree (Kowarik and Säumel 2007). The spread of *A. altissima* has often been associated with natural disturbances (Xi 2008; Maringer et al. 2012; Kasson et al. 2013) or disturbance caused by forest management (Call and Nilsen 2003; Radtke et al. 2013; Berg et al. 2017; Rebbeck et al. 2017). Radtke et al. (2013) found frequent clear-cuts in coppice forests to favour the establishment and spread of *A. altissima* in northern Italy, while the time since the last timber harvest was the best predictor of *A. altissima* presence and density in state forests in Ohio, USA (Rebbeck et al. 2017). Moreover, natural disturbances such as fire (Maringer et al. 2012), windthrow (Xi 2008) or insect defoliation (Kasson et al. 2013) were found to lead to an increase in the abundance and/or the area colonised by *A. altissima*. In particular, light availability (Knapp and Canham 2000; Maringer et al. 2012; Martin et al. 2010; Berg et al. 2017; Rebbeck et al. 2017) and nutrient availability (Soják and Löffler 1988; Berg et al. 2017) were found to increase the growth and abundance of *A. altissima* regeneration.

Study area

The study was conducted in the sweet chestnut (*C. sativa*) forests of southern Switzerland. The climate in the study area is characterized by a mild average annual temperature of ca 12.7 °C and a mean annual precipitation of 1862 mm (climate normal 1981–2010, MeteoSwiss station Locarno-Monti, 383 m a.s.l.). A large amount of precipitation falls in short and heavy spells during the growing season (1023 mm

from May to September) followed by a relatively dry period in winter. The soils are classified as haplic podzol (cryptopodzol) on crystalline bedrock (Blaser et al. 2005).

The studied forests used to be dominated by *C. sativa*, which was introduced by the Ancient Romans more than 2000 years ago (Tinner et al. 1999) and intensively cultivated in monocultures as coppice forests or orchards (Conedera et al. 2004). The cultivation of *C. sativa* dropped in the 1950s as a consequence of a general abandonment of agriculture and the simultaneous spread of the chestnut blight (*Cryphonectria parasitica* (Murr.) Barr.). In the following decades, chestnut forests were increasingly colonised by native (*Fraxinus* spp., *Tilia* spp., *Prunus* spp.) and non-native tree species (*Robinia pseudoacacia* L., *A. altissima*, *Paulownia tomentosa* (Thunb.) Steud.) facilitated by the generally low competitiveness of *C. sativa* (Conedera et al. 2001; Pividori et al. 2005), which was further weakened by repeated outbreaks of pathogens such as the ink disease (*Phytophthora* spp.; Prospero 2017), the chestnut blight (Rigling and Prospero 2018), and since 2009 the arrival of the chestnut gall wasp (*Dryocosmus kuriphilus* Yasumatsu; Gehring et al. 2017).

Study sites

We selected three study sites in southern Switzerland based on an occurrence map of *A. altissima* (Gurtner et al. 2015). We looked for sites at the current distribution frontier of the species with no vegetative regeneration. All sites (named Locarno, Sementina, San Vittore) are situated in the chestnut belt at elevations ranging from 400 to 550 m a.s.l. Their slopes are facing SW to SE with an average inclination of 70° (± 18.0° standard deviation, Fig. 1). In all three sites, *C. sativa* comprises the largest fraction of basal area (77–98%), followed by deciduous *Quercus* spp. (0–15%). All other species have a basal area <5% (*Betula pendula* Roth, *Robinia pseudoacacia* L., *Tilia* spp., *Fraxinus* spp., *Prunus avium* (L.) L., *Sorbus aria* (L.) Crantz, *Paulownia tomentosa* Steud., *Populus tremula* L., *Populus alba* L., *A. altissima*). All studied forests used to be managed as coppices except for a small part (ca 1 ha) of the site in San Vittore, which was managed as a chestnut orchard. In all three sites, no management has taken place since the 1950s apart from occasional cuttings of single trees or small forest patches (<0.2 ha).

To get an overview of the colonization history as well as the existing propagule pressure of *A. altissima* in the study sites, we searched for and mapped all seed-bearing female *A. altissima* within the boundary of the study sites and in a buffer of approximately 300 m around the studied forests. Of all accessible female trees, an increment core was extracted at a height of ca 1.3 m to determine their age. In the site Locarno, only a single female tree was found with an age of ca 18 years. In Sementina, the oldest of the four female trees was ca 27 years old, while the other three were only ca 15 years old. In the site San Vittore, several adult and at
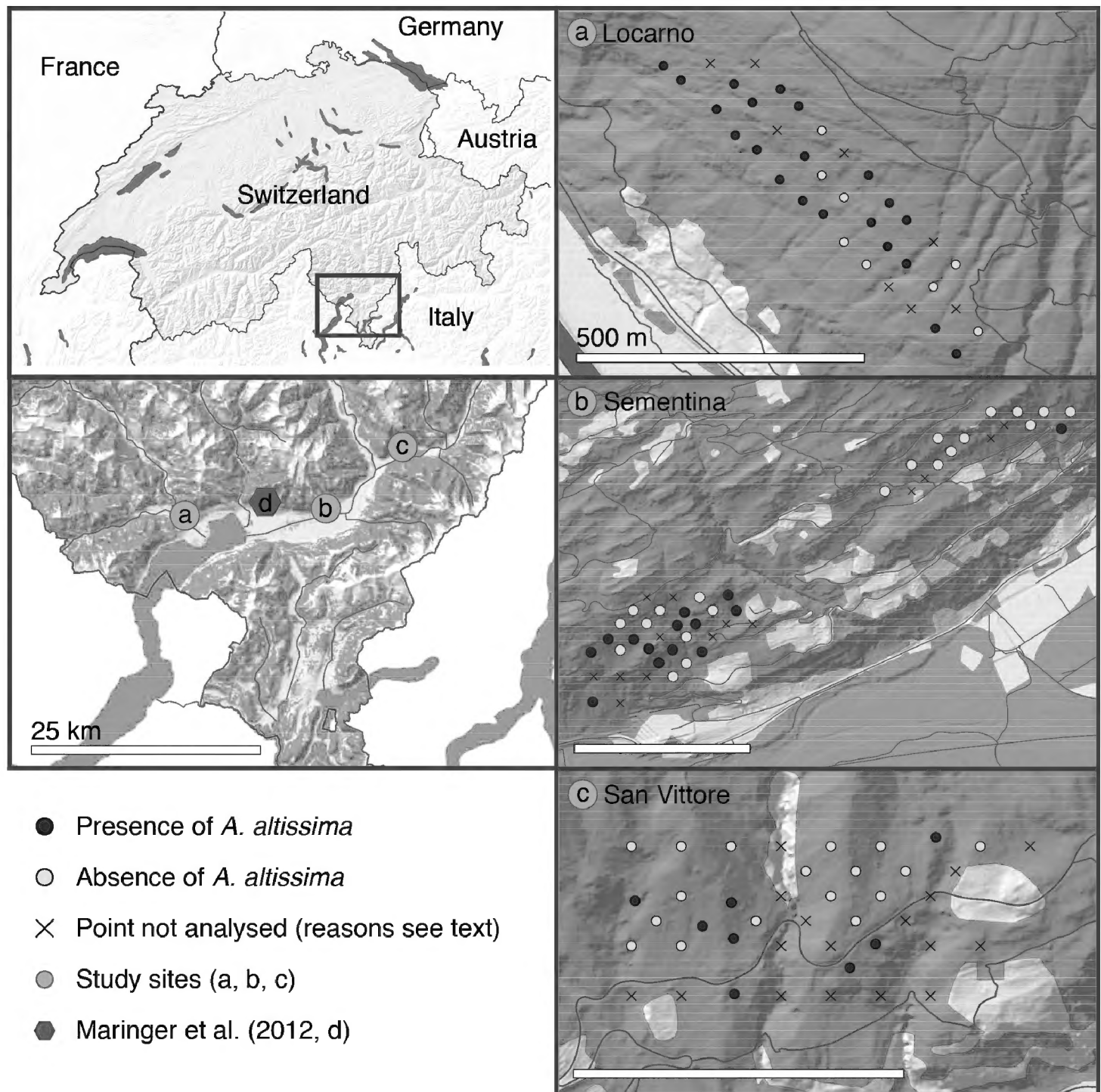
Figure 1. Study area and study sites. Study area in southern Switzerland (left column) and selected study sites: Locarno (a; 46°10'36"N, 8°46'12"E), Sementina (b; 46°10'53"N, 8°58'13"E) and San Vittore (c; 46°14'19"N, 9°04'46"E; right column with scale bars representing 500 m). (d) Represents the study area analysed by Maringer et al. (2012) on the establishment of non-native species after a forest fire, which was used for comparison in this study.

least 40-years-old *A. altissima* trees that grew along the road crossing the study site (Fig. 1) were girdled in 2010 and felled in winter 2014 (Luca Plozza, pers. comm.). About 10 adult trees remained in the forest, of which the oldest female tree was ca 40 years old. Although we searched for seed-bearing female *A. altissima* during the sampling (summer 2015) and in the following winter after leaf shedding, it cannot be ruled out entirely that further and yet undiscovered seed-bearing trees exist in inaccessible parts around the study sites.

Sampling design

We applied a systematic sampling design that was centred on *A. altissima*. An adaptation was necessary to obtain a sufficient number of sampling points with regeneration of *A. altissima*, as the studied forests are located at the distribution frontier where the species occurs at low densities only. To this end, we placed a regular grid with a mesh size of 50 m over all three study sites and defined potential sampling points at the nodes of the grid. At each of these points we searched for *A. altissima* saplings (>40 cm tall and <12 cm DBH) in a circular area of 800 m² (ca 16 m radius) around the sampling points. Plants smaller than 40 cm were not considered to avoid individuals that had germinated in the year of the field survey (Knüsel et al. 2016). This resulted in 44 sampling points with saplings of *A. altissima* in the vicinity (later referred to as *presence points*) and 45 without (later referred to as *absence points*), i.e. a total of 89 sampling points (Fig. 1). These numbers already exclude several sampling points that were inaccessible (*n* = 15), experienced heavy management (*n* = 8, i.e. below a power line and close to a building inside the forest), or were close (<10 m) to a forest road (*n* = 9). In addition, six sampling points were excluded because of mature *A. altissima* (DBH >12 cm) in the 800 m² circle, which may support conspecific regeneration via root grafts (O'Neal and Davis 2015).

At the absence points, two nested, slope-corrected circular plots with sizes of 100 and 200 m² were temporarily installed at the nodes of the grid. At presence points, in contrast, the nested plots were not installed at the nodes of the grid, but were moved to have the nearest *A. altissima* sapling in the centre.

A range of environmental variables were then measured in each plot. First, the light environment was recorded at the plot centre with a hemispherical photograph (Canon EOS 50D camera with a Sigma EX DC 4.5 mm fisheye lens). The photograph was taken horizontally at a height of 1.7 m to avoid shading by small regeneration. If the *A. altissima* sapling representing the plot centre (later referred to as *central A. altissima*) at presence points was taller than 1.7 m it was bent to the forest floor to avoid self-shading. In addition, the age of the central *A. altissima* was assessed by counting growth units (Heuret et al. 2003) for individuals <6 years and by taking an increment core or a stem disc at 40 cm height for older individuals. Furthermore, we excavated the central *A. altissima* to verify its seed origin in case a mature *A. altissima* occurred within 20 m. All excavated central *A. altissima* originated from seeds.

In the 100 m² plot, we surveyed ground cover as well as seedlings (10–40 cm tall) and saplings (>40 cm tall) of all tree species. Percentage cover of bare soil (later referred to as *mineral soil cover*), litter, herbs and shrubs (later referred to as *vegetation cover*), coarse woody debris and vegetation-free rock (later referred to as *rock cover*) were assessed visually in 10% classes. Ground cover values were assessed so that they added up to 100%. For tree seedlings, the species and the presence of recent (i.e., last three years) browsing damages were noted. For saplings, we additionally recorded height, DBH and damage by fraying (only for saplings >130 cm tall).

In the 200 m² plot, we assessed stand structure and signs of management (i.e., presence of tree stumps). For all trees and coppice shoots or stools (DBH >12 cm), DBH, height and the vitality class following Tinner et al. (2010) were recorded.

Establishment models

Model types

We used two types of multiple regression models to analyse *A. altissima* establishment. First, we used logistic models (LOG) to analyse the presence or absence of *A. altissima* saplings. Second, we used negative binomial models (NB) to analyse the abundance (number) of *A. altissima* saplings (see Methods S1 for details).

Explanatory variables

The light environment was characterized by the Gap Light Index (GLI), which integrates diffuse and direct irradiation over a growing season. GLI was calculated from the hemispherical photographs with the program *Hemisfer* (www.schleppi.ch/hemisfer; Schleppi et al. 2007). As an additional measure, we quantified canopy closure, i.e. the proportion of the sky covered by vegetation when viewed from a single point (Jennings et al. 1999; Gonsamo et al. 2013). Canopy closure was further used as a single explanatory variable in a separate simple LOG model, since it represents a more intuitive and easily obtainable measure of the light environment that can be estimated visually by practitioners. Based on this simple model, we calculated a threshold canopy closure value that best differentiated the presence or absence of *A. altissima* saplings by optimizing for the sum of sensitivity and specificity based on the ROC curve with the *R* function *coords* in the *R* package *pROC* (Robin et al. 2011).

Three of the five assessed ground cover variables, mineral soil, litter, and rock cover were used as explanatory variables (Table 1). Vegetation cover was excluded due to a variance inflation factor (VIF) >5, calculated with the *vif* function in the *R* package *car* (Fox and Weisberg 2011). Coarse woody debris was excluded due to the small variance in the data (Table 1) and a lacking ecological justification, since no regeneration growing on woody debris was found (personal observation). Furthermore, we approximated propagule pressure by the minimal distance of each sampling point to the nearest seed-bearing tree (later referred to as *seed source*). The distance to the next seed source was calculated using ArcGIS. In addition, we characterised stand density by the total sum of living basal area (m^2 ha^{-1}) of all trees on the plot above 12 cm DBH. Due to the high browsing pressure on competing tree species (but not on *A. altissima*), we calculated an average proportion of browsed co-occurring species (excluding *A. altissima*) for each sampling point. Finally, we analysed interactions of saplings of *A. altissima* with saplings of other tree species. To this end, we selected the number of seedlings and the number of saplings of the four most abundant species as additional explanatory variables. Moreover, we selected the sum of living basal area of the four tree species with the highest total basal area to analyse interactions with canopy tree species. The number of other tree species' seedlings and saplings, as well as the living basal area were not used in the process of model selection, but were only added to the most parsimonious models after model selection.

All continuous variables were standardized before running the models by subtracting the mean and dividing the result by the standard deviation.

Table 1. Environmental parameters recorded for the establishment models.

Continuous predictors	Mean (SD)	Range
Light environment:		
Gap light index (GLI)	21 (14.6)	4–73
Ground cover:		
Mineral soil cover (%)	15 (12.4)	0–52
Litter cover (%)	32 (20.8)	0–85
Rock cover (%)	18 (13.9)	0–70
Coarse woody debris cover (%)	5 (6.1)	0–32
Vegetation cover (%)	29 (24.7)	0–92
Propagule pressure:		
Distance to seed source (m)	127 (65.1)	15–303
Stand characteristics:		
Basal area per plot (m² ha⁻¹)	36 (21.3)	5–121
Browsing:		
Browsed competitors (%)	40 (18.0)	0–100
Categorical predictors	**Levels**	***n***
Site	Locarno	29
	San Vittore	25
	Sementina	35

Bold labels indicate predictors that were used for model selection.

Model selection

Starting with the eight selected variables (Table 1), we generated a full submodel set with the *dredge* function in the *R* package *MuMIn* (Bartoń 2018). Three main models were chosen for reporting: (1) null model (later referred to as NB_{null}, LOG_{null}), (2) most parsimonious model of those models that differed by less than 2 AIC_C points compared to the model with the lowest AIC_C score (later referred to as NB_{pars}, LOG_{pars}), (3) average of all models within 2 AIC_C points (later referred to as NB_{avg}, LOG_{avg}). All models within 4 AIC_C points as well as the average thereof can be found in Tables S1–S4.

For the averaging of all models within 2 AIC_C points, we used the zero method to compute parameter estimates (Burnham and Anderson 2002; Nakagawa and Freckleton 2010), where a parameter estimate of zero is added for a parameter not occurring in a model selected for averaging. In addition, a relative importance value for each explanatory variable occurring in at least one of the averaged models was calculated. It represents the fraction of models used for averaging in which a certain variable occurred.

Model performance

Goodness-of-fit of the models was assessed by comparing the most parsimonious models against the null model with a Chi-squared test. For the LOG models we further calculated AUC values with the *R* package *pROC* (Robin et al. 2011) to quantify the predictive power of the models. As no similar measure exists for NB models, we computed the Pearson correlation of the observed number of *A. altissima* saplings versus the predicted number using NB_{pars}.

Comparison with post-fire establishment

To discriminate factors driving the establishment of *A. altissima* after a forest fire (Maringer et al. 2012) versus in recently undisturbed stands (this study, no forest management or other large-scale disturbances for the last ca 60 years), we re-analysed the data of Maringer et al. (2012). The authors studied the establishment of non-native species in plots affected by a forest fire four years before and in adjacent control plots (Maringer et al. 2012). The study was conducted in the same study region (Fig. 1).

In particular, we aimed at quantifying differences in ground cover and light availability in presence and absence points in this study and in fire affected plots in Maringer et al. (2012). Due to deviations in the sampling protocols we did not directly compare values between the studies, but used two-sided Wilcoxon tests instead to quantify differences within but not across the studies. Ground cover values have been assessed in a circle of 200 m^2 size in Maringer et al. (2012) as opposed to a 100 m^2 circle in our study. In addition, Maringer et al. (2012) assessed herb, fern and shrub cover separately. Hence, vegetation cover in this study (sum of herb and shrub cover) was compared to herb cover only of Maringer et al. (2012). Further, canopy closure in Maringer et al. (2012) was measured from eight photographs taken in subplots of the 200 m^2 plot, whereas in our study it was calculated from a single hemispherical photograph taken at each sampling point.

Results

Presence and abundance of regeneration

The presence points were on average slightly closer to seed sources (118 m, ± 61.3 m standard deviation) than the absence points (136 m, ± 68.1 m), however not significantly ($P > 0.2$). In the 44 presence points, a total of 243 saplings of *A. altissima* were recorded. They had a mean height of 224 cm (± 179.9 cm), a mean DBH of 1.0 cm, and a mean age of 4 years (± 1.8 yr), with a maximum of 11 years. When present, *A. altissima* saplings often dominated the regeneration at the sampling point (57% ± 31.3% of all saplings, Table 2). The four most abundant saplings of other species were *C. sativa* (total = 181), *R. pseudoacacia* (80), *Fraxinus* spp. (50) and *S. aria* (31).

In addition, we recorded a total of 188 seedlings of *A. altissima*, accounting on average for 16% (± 18.1%) of all seedlings at the presence points (Table 2). The four most abundant seedlings of other species were *Fraxinus* spp. (total = 1560), *Quercus* spp. (1241), *C. sativa* (1186) and *R. pseudoacacia* (202).

Only *A. altissima* showed an increasing relative frequency of individuals with increasing height (Fig. 2). In contrast, the most frequent co-occurring species at the earliest stages, such as *Quercus* spp. and *Fraxinus* spp., featured a strong reduction in stem numbers with increasing height.

Table 2. Presence and abundance of regeneration. Shown are seedlings (10–40 cm tall) and saplings (>40 cm tall and <12 cm DBH) of *A. altissima* and the four most abundant co-occurring seedlings or saplings. Values are averages per sampling point, with standard deviations in parentheses.

Class	Species	Sampling points			
		With *A. altissima* saplings		Without *A. altissima* saplings	
		n*ha⁻¹	proportion per sampling point (%)	n*ha⁻¹	proportion per sampling point (%)
Seedlings	*A. altissima*	494 (513)	16 (18.1)	163 (177)	4 (6.5)
	Fraxinus spp.	4023 (11312)	35 (26.1)	1082 (1812)	20 (18.1)
	Quercus spp.	1161 (1375)	28 (22.4)	2146 (3329)	37 (31.0)
	C. sativa	1068 (1377)	20 (18.6)	1912 (3174)	42 (27.5)
	R. pseudoacacia	563 (392)	15 (10.5)	500 (831)	10 (8.7)
Saplings	*A. altissima*	560 (603)	57 (31.3)	–	–
	C. sativa	391 (429)	30 (23.3)	465 (470)	72 (32.0)
	R. pseudoacacia	492 (776)	26 (20.3)	300 (490)	18 (12.4)
	Fraxinus spp.	257 (234)	16 (9.6)	275 (236)	45 (46.1)
	S. aria	500 (693)	23 (31.6)	229 (138)	46 (29.1)

Proportions per sampling point are an average over all sampling points in which the respective species occur.
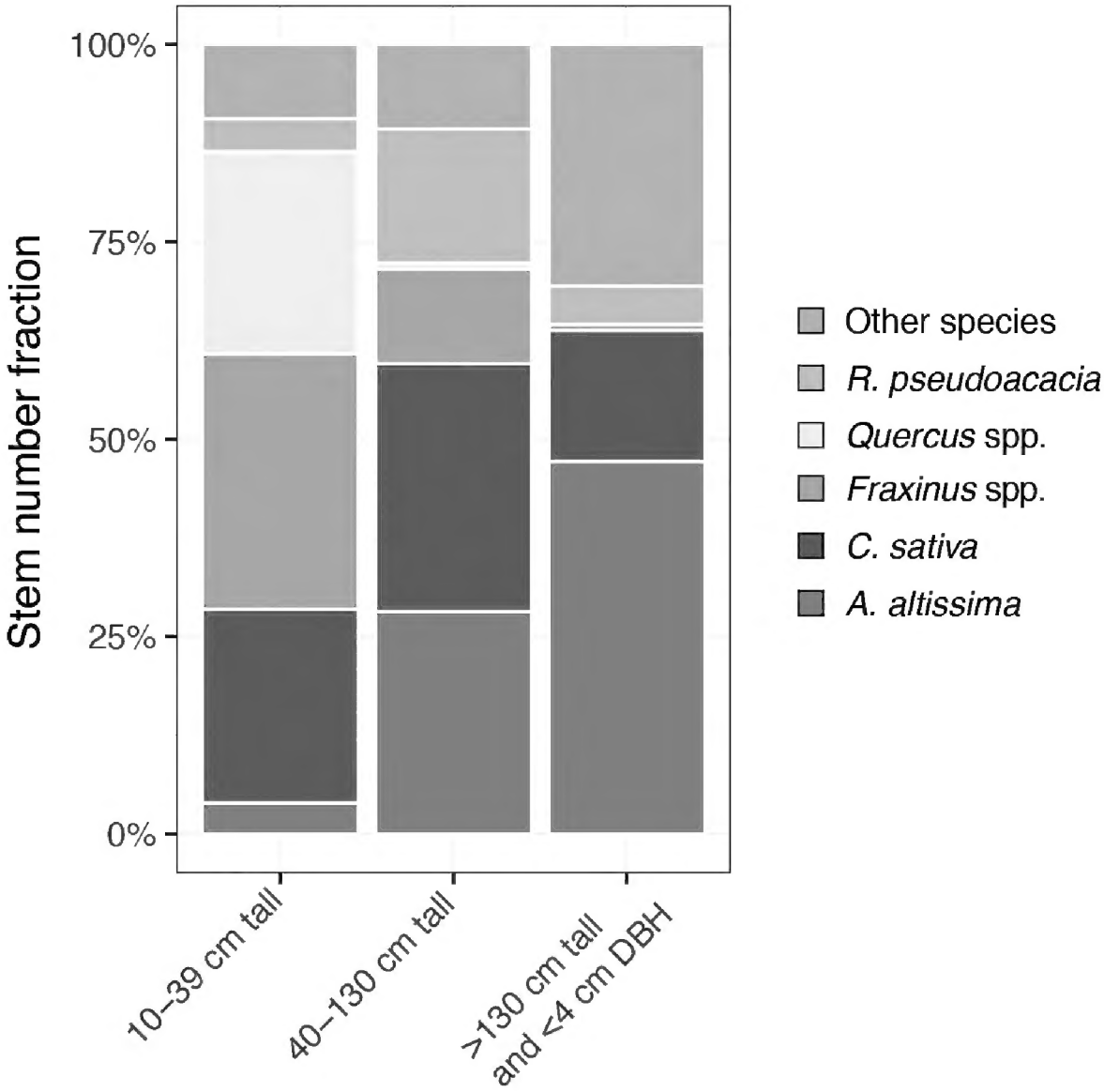

Figure 2. Fractions of stem numbers per species for three different height classes. Data were pooled from all three sites.

Establishment models

Drivers of *A. altissima* occurrence

The occurrence of *A. altissima* saplings was positively ($P < 0.05$) affected by rock cover and negatively ($P < 0.001$) by litter cover in LOG_{pars} (Table 3). LOG_{pars} fitted the data significantly better ($P < 0.001$) than LOG_{null} as indicated by a Chi-squared test. LOG_{avg} identified rock cover as the only significant variable ($P < 0.05$), which also had the highest relative importance. Additionally, LOG_{avg} identified the GLI, distance to seed source, mineral soil cover and site as explanatory variables, which were not included in LOG_{pars}. However, only GLI and distance to seed source were included in a larger number of averaged models (>60%). Both LOG_{pars} and LOG_{avg} had similar AUC values (0.88 and 0.91, respectively).

Table 3. Results of the logistic models of the occurrence of *A. altissima* saplings. The null model (LOG_{null}), the most parsimonious model (LOG_{pars}) as well as an average of all models ($n = 8$) within 2 AIC_C points (LOG_{avg}) are shown. Significant predictors are written in bold, values in parentheses represent standard errors.

	LOG_{null}	LOG_{pars}	LOG_{avg}
(Intercept)	−0.05	−0.19	0.21
	(0.21)	(0.29)	(0.65)
Rock cover (%)		**0.74***	**0.82***
		(0.36)	(0.41)
Litter cover (%)		**−1.86*****	−1.11
		(0.42)	(0.71)
Gap Light Index (-)			0.92
			(0.68)
Distance to seed source (m)			−0.44
			(0.43)
Mineral soil cover (%)			0.12
			(0.25)
Site - San Vittore			−0.19
			(0.51)
Site - Sementina			−0.52
			(1.00)
AIC_C	123.99	82.41	–
AUC	0.50	0.88	0.91
Relative importance			
Rock cover			1.00
Litter cover			0.87
Gap Light Index			0.83
Distance to seed source			0.69
Mineral soil cover			0.27
Site			0.26

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

The three most important variables according to LOG_{avg}, i.e. rock cover, litter cover and GLI, showed significant differences ($P < 0.01$) between presence-and absence points (Fig. 3a, b, e, red boxes). In addition, vegetation cover, which was excluded from the models due to multicollinearity, was significantly higher ($P < 0.01$) at presence points (Fig. 3d). As a more intuitive measure, the light environment was additionally characterized by canopy closure (Fig. 3f). At a threshold value of 86% canopy closure, the highest correct classification rate could be achieved based on canopy closure alone (Fig. 3f, red dashed line).

Drivers of *A. altissima* abundance

According to NB_{pars}, the abundance of *A. altissima* saplings was significantly positively affected by GLI and the percentage of browsed competitors, whereas litter cover had a significantly negative effect (Table 4). As for the logistic model, NB_{pars} fitted the data significantly better ($P < 0.001$) than NB_{null}, but displayed a poor predictive power with a low correlation ($r = 0.17$) between observed and predicted numbers of *A. altissima* saplings (Fig. S1).

NB_{avg} identified the percentage of browsed competitors, GLI and litter cover as the most important variables as well, supplemented by mineral soil cover, total basal area and rock cover. However, the influence of total basal area and rock cover were marginal only (Table 4).

Browsing and fraying

Overall, *A. altissima* regeneration (10–300 cm tall) experienced less ($P < 0.01$) browsing damage compared to the four most frequent other species (*Fraxinus* spp., *C. sativa*, *Quercus* spp. and *R. pseudoacacia*) and an average of all other species (Fig. 4).

Compared to the two species with most abundant saplings taller than 130 cm (*C. sativa* and *R. pseudoacacia*) as well as an average over all other species, *A. altissima* was frayed significantly less (56% ± 33% standard deviation, $P < 0.05$) than *C. sativa* (81% ± 27%) but did not differ significantly ($P > 0.4$) from *R. pseudoacacia* (75% ± 35%) or an average of all other species (52% ± 31%, Fig. S2).

Comparison with post-fire establishment

Two of the three most important variables for the occurrence of *A. altissima* saplings identified in this study, litter cover and light availability, also differed significantly ($P < 0.01$) between presence- and absence points in a study conducted after a forest fire (Maringer et al. 2012, Fig. 3b, f). Mineral soil cover, in contrast, was significantly higher ($P < 0.01$) in presence points after fire (Maringer et al. 2012), but not in this
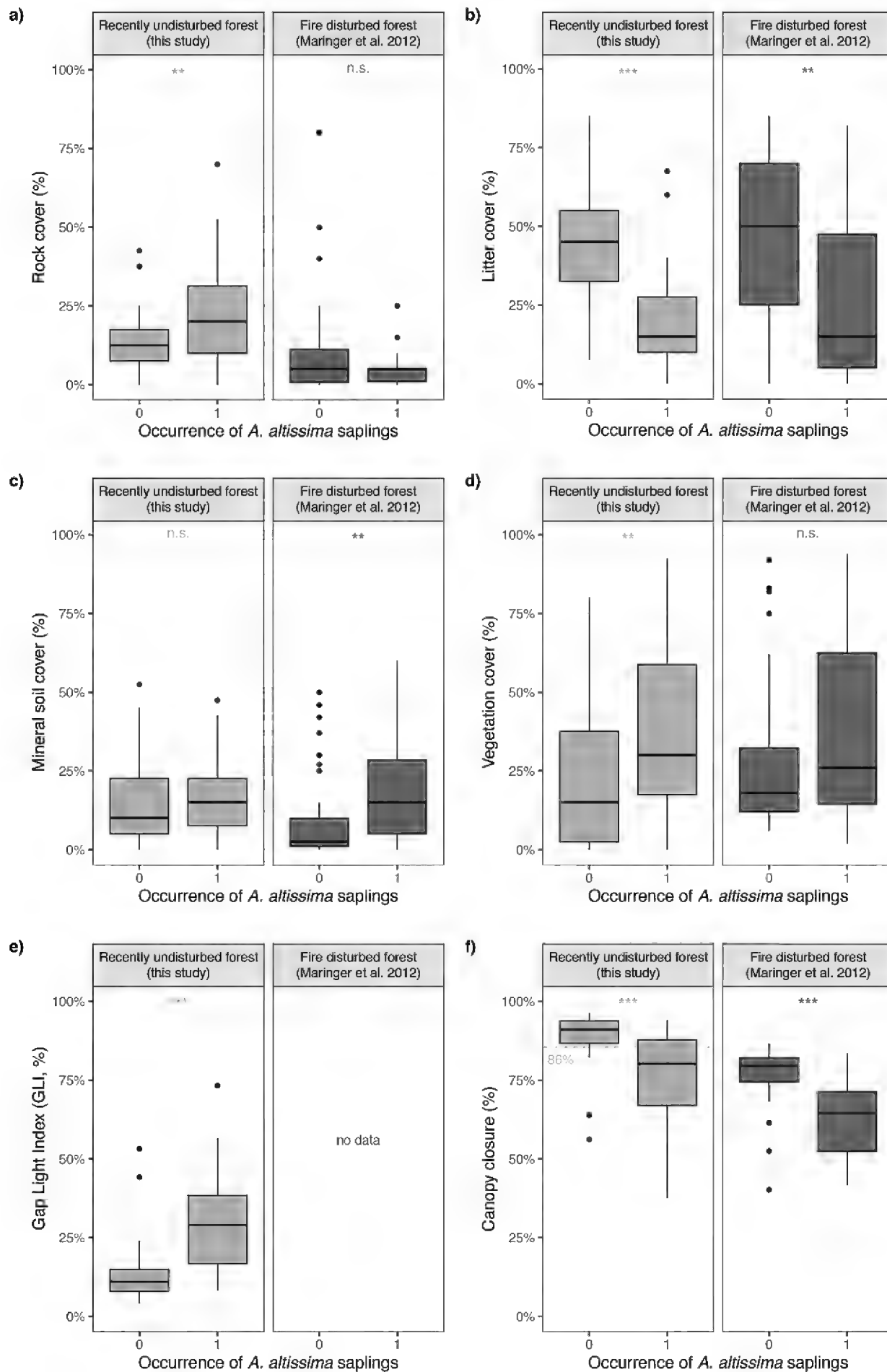
Figure 3. Comparison of ground cover (**a–d**) and light environment (**e, f**) between sampling points with or without saplings (>40 cm tall and <12 cm DBH) of *A. altissima*. Values originate from recently undisturbed forests (this study), and from a forest analysed four years after a fire (Maringer et al. 2012). The dashed line in (**e**) shows a threshold value that is optimized for sensitivity and specificity to distinguish sampling points with or without saplings of *A. altissima* in recently undisturbed forests. Asterisks indicate significant differences between sampling points with and without saplings of *A. altissima* (** $P < 0.01$, *** $P < 0.001$). See text for differences in the sampling procedure between this study and Maringer et al. (2012).
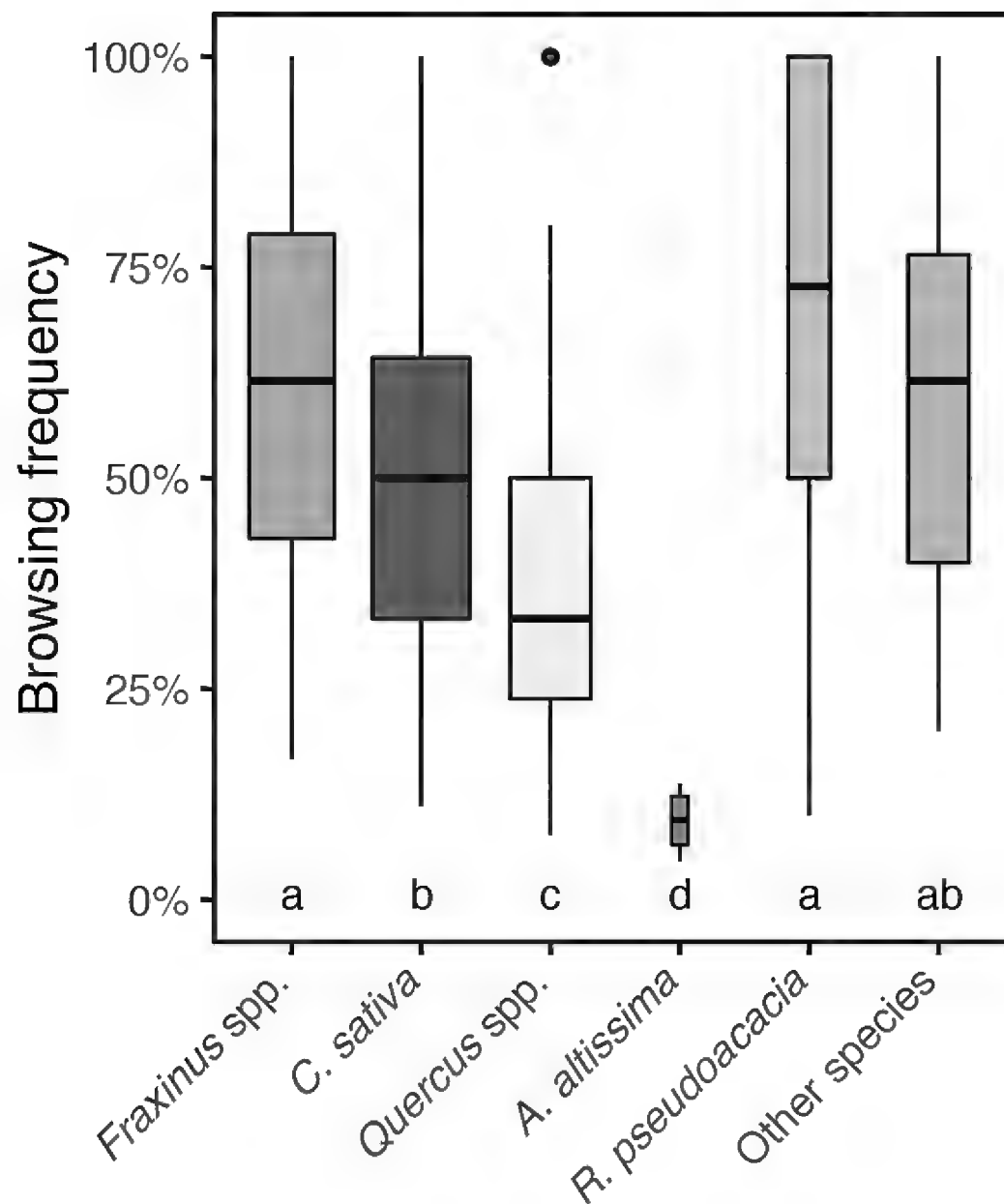
Figure 4. Proportion of browsed regeneration. Browsing damages were recorded on saplings 10–300 cm tall for the three most recent years. Widths of the bars are proportional to the number of individuals recorded ($n > 360$). Different lowercase letters indicate significant ($P < 0.05$) differences between proportions.

study (Fig. 3c). In addition, rock cover was generally lower in the area studied by Maringer et al. (2012) and did not differ significantly between presence- and absence points, while the difference was significant ($P < 0.01$) in this study (Fig. 3a). Moreover, vegetation cover was higher in presence points in both studies (Fig. 3d), but only differed significantly ($P > 0.01$) in this study.

Interactions with other species

The number of *A. altissima* saplings was significantly negatively ($P < 0.05$) correlated with the number of *S. aria* saplings only (Table S6). However, *S. aria* was merely present in 10 sampling points, with a maximum of 13 saplings at one sampling point (cf. Table 2). The three species with most abundant saplings (*C. sativa*, *R. pseudoacacia* and *Fraxinus* spp.), in contrast, were not significantly related ($P > 0.2$) to the number of *A. altissima* saplings.

Table 4. Results of the negative binomial model of the number of *A. altissima* saplings. The null model (NB$_{null}$), the most parsimonious model (NB$_{pars}$) as well as a model average of all models (n = 6) within 2 AIC$_C$ points (NB$_{avg}$) are shown. Significant predictors are written in bold, values in parentheses represent standard errors.

	NB$_{null}$	NB$_{pars}$	NB$_{avg}$
(Intercept)	**1.01*****	**0.53****	**0.51****
	(0.21)	(0.19)	(0.19)
Gap Light Index (-)		**0.70****	**0.75****
		(0.24)	(0.26)
Browsed competitors (%)		**0.45***	**0.45***
		(0.18)	(0.18)
Litter cover (%)		**–0.64***	–0.53
		(0.28)	(0.33)
Mineral soil cover (%)			0.23
			(0.23)
Total basal area (m²ha⁻¹)			0.05
			(0.13)
Rock cover (%)			0.01
			(0.07)
AIC$_C$	349.95	330.73	–
Relative importance			
Gap Light Index			1.00
Browsed competitors			1.00
Litter cover			0.89
Mineral soil cover			0.61
Total basal area			0.24
Rock cover			0.11

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

The number of *A. altissima* saplings was positively ($P < 0.001$) correlated with the number of seedlings of *R. pseudoacacia* and *Fraxinus* spp., while there was no significant relationship ($P > 0.5$) with the other two most frequent seedling species, *C. sativa* and *Quercus* spp. (Table S5).

The amount of basal area of live trees of the four most prominent tree species (*C. sativa*, *Quercus* spp., *B. pendula* and *R. pseudoacacia*) at presence points did not show a significant relationship ($P > 0.05$) with *A. altissima* sapling density (Table S7).

Discussion

Regeneration models
Drivers of *A. altissima* occurrence

The occurrence of *A. altissima* saplings was mainly favoured by high rock cover, low litter cover and high light availability (Table 3). A beneficial effect of a high rock cover on the presence of *A. altissima* has not been found in other studies that analysed the

establishment of the species in forests (Maringer et al. 2012; Radtke et al. 2013). However, *A. altissima* is known to thrive in ruderal urban sites (Celesti-Grapow and Blasi 2004; Kowarik and Säumel 2007) that partly resemble rocky forest patches. Rock cover has been suggested to reduce competition and serve as a refuge for early successional species (Frelich and Reich 2002), even more if they are drought tolerant (Plieninger et al. 2010). Both effects may partially explain the association of *A. altissima* with rocky forest patches.

The negative effect of litter cover for the occurrence and the abundance of regeneration of *A. altissima* may have been caused by a delay in germination and an increased invertebrate herbivory and seedling mortality, as found in an early successional site (Facelli and Pickett 1991; Facelli 1994). Similarly, Kostel-Hughes et al. (2005) found reduced robustness of seedlings that emerged from deep litter (ca 5 cm deep) in an experimental study, although there was no difference in the probability of emergence between different litter treatments (no litter, 1–2 cm and ca 5 cm deep litter).

As expected, light availability played a major role for the occurrence of the early successional *A. altissima*. Although the species is able to persist in low light levels for several years (Knapp and Canham 2000; Knüsel et al. 2016), most of the presence points experienced light levels above 10% GLI (Fig. 3e). A study of Martin et al. (2010) conducted in forests in north-western Connecticut (USA) found that radial growth of *A. altissima* exceeded native regeneration at levels >10% of full sunlight (GLI), but not at light levels below 3%. However, we did not measure such low light levels in this study (Fig. 3e). Moreover, Huebner et al. (2018) found canopy closure of ca 85% and above to reduce the establishment probability for *A. altissima*. The threshold suggested by Huebner et al. (2018) also matches the 86% canopy closure level found in this study (Fig. 3f, red dashed line), at which the probability of false positive and false negative classifications of *A. altissima* occurrence was minimal.

Drivers of *A. altissima* abundance

The models for the abundance of *A. altissima* saplings had a much lower predictive power than the occurrence models, which implies that the following interpretations represent tendencies only. While high light availability and low litter cover were also important for the density of *A. altissima* regeneration, rock cover did not influence sapling abundance. This might be related to the lower availability of suitable sites for establishment in rocky forest patches (Frelich and Reich 2002). In contrast, sapling density of *A. altissima* was positively influenced by an increased cover of mineral soil (Table 4, Fig. 3c), which is known to be an important factor for the establishment of many light-demanding early successional tree species (Shields et al. 2007; Zouhar et al. 2008), including *A. altissima* (Call and Nilsen 2003; Martin and Canham 2010). Furthermore, the observed high browsing pressure on competitors may have indirectly favoured the largely unbrowsed regeneration of *A. altissima* through reduced competition.

However, the distribution of tree species is determined not only by the availability of suitable microsites for their establishment, but also by seed production and dispersal

(Nathan and Muller-Landau 2000; Turnbull et al. 2000). Limitations in propagule pressure are often particularly important for expanding non-native tree species (Pyšek et al. 2009; Terwei et al. 2013; Conedera et al. 2017; Sullivan and Franco 2017; Dyderski and Jagodziński 2018). Accordingly, the distance to the next seed source played a role for the occurrence of *A. altissima* (Table 3), which is in line with previous studies (Radtke et al. 2013; Höfle et al. 2014). Thus, a further increase in seed-bearing female *A. altissima* is likely to lead to an increase in the distribution range of the species. Yet, the distance to the next seed source was not important for the density of *A. altissima* (Table 4). This may suggest that the density of *A. altissima* is mainly driven by the amount of suitable establishment sites in case seeds are available. Nevertheless, seed addition experiments would be required to quantify the relative importance of seed limitation for the occurrence and density of *A. altissima* in the studied forests (Turnbull et al. 2000).

Vegetation cover, which was excluded from the models due to multicollinearity with light availability and litter cover, was significantly higher at presence points (Fig. 3d). This may contradict the oftentimes reported negative effect of herbs and shrubs on the establishment of tree regeneration (Maguire and Forman 1983; Picon-Cochard et al. 2006). However, as high light availability tends to simultaneously enhance both the amount of vegetation (Vockenhuber et al. 2011) and the probability of occurrence and abundance of *A. altissima* (Tables 3, 4), high vegetation cover may rather be the consequence of suitable germination conditions. Nevertheless, it is possible that very high vegetation cover (≥75%) hindered the establishment of *A. altissima* at two sampling points with ample light availability (Fig. 3e, outlier points on the left). Yet, *A. altissima* regeneration was still present at three out of five sampling points with vegetation cover ≥75%, probably owed to its fast juvenile height growth (Knapp and Canham 2000; Martin et al. 2010). Hence, we surmise that the role of vegetation cover for the establishment of *A. altissima* may be different depending on the timing of its development and its coincidence with seed rain.

We did not consider soil characteristics as *A. altissima* is known to tolerate a broad range of soil conditions (Kowarik and Säumel 2007). In other studies, *A. altissima* occurred slightly more often on moister soils (Radtke et al. 2013) and was associated with sites with high indicator values for nutrients (Berg et al. 2017). However, soil characteristics were not identified as the main factors influencing the establishment of *A. altissima*.

Browsing and fraying

Ailanthus altissima suffered almost no damage from ungulate browsing compared to co-occurring regeneration (Fig. 4), which agrees with findings of Maringer et al. (2012). We hypothesize that browsing may enhance the establishment success of *A. altissima* through reduced competition by co-occurring regeneration, as suggested by the abundance models. Reduced herbivory by ungulates or insects is common for many novel non-native species and may influence successional pathways of colonised forest stands (Cappuccino and Carpenter 2005; Knapp et al. 2008). However, differences in herbivore damage are thought to decrease with time since introduction (Brändle et al. 2008; Schilthuizen et al.

2016). Furthermore, results from Hungary (Mátrai et al. 2004) and the USA (Hunter 1995; Carter and Fredericksen 2007) demonstrate that *A. altissima* is sometimes browsed as frequently as co-occurring trees. In addition, fraying damages on larger regeneration, which were to our knowledge considered for the first time in this study, were as frequent on *A. altissima* as on other species (Fig. S2). However, fraying did not seem to cause mortality, as several saplings with sealing callus growth and wound closure were found. This is in line with findings of Gurtner (2015) in the study region.

Comparison with post-fire establishment

Forest fires temporarily increase the availability of light and nutrients, and reduce competition (Tyler and D'Antonio 1995; Keeley et al. 2003), which tends to promote the establishment of *A. altissima* (Maringer et al. 2012; Crandall and Knight 2018). These same factors, i.e. high light availability and reduced competition via high rock cover or browsing on competing regeneration were also important for the establishment of *A. altissima* in recently undisturbed forests analysed here. Furthermore, low litter cover seemed to be similarly important for the establishment of *A. altissima* after a fire and in recently undisturbed forests. Moreover, *A. altissima* seems to benefit from the higher availability of mineral soil after a fire for its establishment. Based on the similar patterns in the establishment drivers of *A. altissima* in fire-disturbed and recently undisturbed forests (Fig. 3), we conclude that *A. altissima* follows the same establishment strategy in both cases. This is in line with findings of Martin et al. (2010), who suggest that *A. altissima* is restricted by a trade-off between low light survivorship and high light growth also when growing in closed-canopy forests, unlike other non-native tree species such as *Acer platanoides* L. (Martin and Marks 2006; Martin et al. 2010; Shouman et al. 2017). While early generative regeneration of *A. altissima* may only persist for an average of three years at low light levels (< 5% GLI; Martin et al. 2010; Knüsel et al. 2016), *A. platanoides* showed almost no mortality at such light levels after five years (Martin et al. 2010), but was still able to grow at similar rates once released from shade (Martin and Marks 2006; Martin et al. 2010; Shouman et al. 2017). However, the strong vegetative regeneration potential of *A. altissima*, which was not considered in this study, may enable the species to increase its persistence in unfavourable conditions after it successfully established in a forest stand (Kowarik 1995; Knüsel et al. 2016).

Interactions with other species

Due to the early successional character of both *A. altissima* and *R. pseudoacacia* (Radtke et al. 2013; Berg et al. 2017), we expected a positive interaction between these species, as observed by Call and Nilsen (2003). However, only seedlings but not saplings of *R. pseudoacacia* were positively associated with *A. altissima* saplings (Tables S5, S6). This may be related to the high browsing pressure on *R. pseudoacacia* (Fig. 4) that may have strongly reduced the number of saplings of *R. pseudoacacia* (Fig. 2).

Future development of analysed forest stands

The increasing relative abundance of *A. altissima* with increasing development stage (Fig. 2) suggests that the fraction of basal area of *A. altissima* will increase in the analysed forests. Several factors may further favour the future establishment and spread of *A. altissima*. First, an increase in the number of seed-bearing trees may augment both the occurrence and abundance of *A. altissima*, as the dispersal of non-native species is oftentimes limited by propagule pressure (Křivánek et al. 2006; Edward et al. 2009). Second, ungulate browsing may continue to act stronger on co-occurring species, thereby reducing understorey competition for *A. altissima*. Third, natural disturbances such as fire, windthrow or uprooting are expected to increase with climate change (Vogt et al. 2006; Pezzatti et al. 2016), thus creating suitable establishment conditions for *A. altissima* (Martin et al. 2010). Fourth, the high drought tolerance of *A. altissima* already at the sapling stage (Trifilò et al. 2004) may make this species less vulnerable to anticipated prolonged droughts (CH2011 2011; Lindner et al. 2010). Yet, this study only focused at the first generation of *A. altissima*. The transition from the first established canopy trees to the next generation can be particularly important for future forest succession, as seen for declining early-successional *R. pseudoacacia* in northern Italy (Motta et al. 2009).

Conclusions

High light availability, low litter cover and to a lesser degree high rock cover resulted as the most important factors determining the occurrence and abundance of *A. altissima* regeneration in forests lacking of recent large scale disturbances like fire or coppice management (research question i). Interestingly, very similar factors were also important for the establishment of *A. altissima* after a disturbance (research question ii), suggesting a consistent establishment strategy across sites with different disturbance intensities. Thus, light availability remains a key factor that controls the establishment and spread of the species, particularly for generative regeneration analysed in this study.

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Supplementary material 1

Justification for models used on the abundance of *A. altissima*

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Data type: (models)

Explanation note: We used models with a negative binomial distribution to characterize the abundance of *A. altissima* saplings.

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